

VI. *Observations on Immature Sexuality and Alternate Generation in Insects.* By B. T. LOWNE, M.R.C.S. Eng.

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WHILST in Palestine, in 1864, about the 23rd of January, I was encamped with the Rev. H. B. Tristram and party at Enjedi, where I found a large black and yellow species of *Petasia* (*Orthoptera*), both in its larval and imaginal forms, in abundance, feeding upon the leaves of *Calotropis procera*. I cannot give the specific name of the insect, and I believe it has not hitherto been described.

I was surprised to find the larvæ of this insect copulating in considerable numbers. Until lately, I knew of no similar case, but my friend, Dr. J. A. Power, tells me that *Ischnodemus sabuleti* is frequently taken in the same condition, whilst in the so-called pupa-state.

When in Australia, ten years ago, I remember observing numerous individuals of a large wingless *Blatta* in the same condition, but this observation has evidently a totally distinct value, as the *Blatta* in question is not known to me ever to produce wings: hence this is only a similar phenomenon to that observed in the *Cimex lectularius*, an apterous, or more strictly speaking, a larval form in a sexually mature condition.

The following facts, also communicated to me by Dr. J. A. Power, seem to me to unite these phenomena by transitional forms. Several species of *Hemiptera*, as, for instance, *Bryocoris pteridis*, although sexually mature, have a very immature or undeveloped appearance; others, as all the British species of *Nabis*, rarely attain their true imaginal characters in either sex; the female of *Sphyraccephalus ambulans*, which is, as a rule, apterous, has been known in one or two instances only, to be furnished with wings, so that this may be considered as a parallel instance; and, lastly, both sexes of *Velia* are almost always apterous, although they occasionally produce wings.

I have not included in this list cases in which the females only are constantly apterous, because this condition may arise from other causes; but where either one

or both sexes occasionally produce wings, I think we see forms intermediate between apterous, and winged sexually mature ones.

Two views may be taken of the significance of these facts. We may see a transitional condition between a larva like progenitor and an imaginal descendant, or we may see a transition from a winged to an apterous perfect insect.

My own belief is, that we see a transition from a winged to an apterous mature form, and this belief is based on the following facts.

Firstly; that larvæ have been observed copulating, and that there is a decided tendency in many animals for the sexual organs to attain maturity before the animal attains all its adult characters.

Secondly; the rare appearance of wings in many *Hemiptera*, especially in the female of *Sphyracephalus ambulans*, appears more like reversion to a lost ancestral form than a tendency to develop a winged one.

Thirdly; because the sexual organs of insects first appear at a very early period of life, and undergo, in some instances at least, gradual development, until the insect arrives at maturity, although all the other organs undergo a very remarkable metamorphosis. Indeed there is good reason to believe, that the remarkable larval reproduction of *Cecidomyiidae*, depends on the premature development of the sexual organs in the larva.

On the other hand, the principal objection to this view that has occurred to my mind is, that the larva of the *Ametabola* is usually believed to have existed in a mature condition before any winged insects had been developed. Fritz Müller says, "It seems to me, that valid reasons may be brought up in favour of the opinion, that the most ancient insects approached more nearly to the existing *Orthoptera*, and, perhaps, to the wingless *Blattidae*, than to any other existing order." And although Gerstäcker and others have shown, very conclusively to my mind, that the larval forms of the *Metabola* are not direct or inherited, but indirect or acquired, I am not aware that any one has advanced this hypothesis with regard to the metamorphosis of the *Ametabola*.

I shall now consider, at some length, the facts bearing upon the above reasons in favour of, and against the views I have advanced.

First. With regard to the early sexual maturity of larval forms.

I have already given instances, in the sexual condition, of the larva of *Petasia* and *Ischnodemus*, but one of the most striking facts of this kind is said to occur amongst the *Echinodermata*: last summer, Mr. Alex. Agassiz related the instance to which I refer, at a meeting of the Royal Society, at the conclusion of one of Dr. Carpenter's "Papers on Deep Sea Life." It was this remark of Mr. Agassiz that first led me to suspect that the wingless forms of *Hemiptera* and *Orthoptera* might have arisen from early maturity of the sexual organs.

Mr. Agassiz stated, that the young of a Mexican *Echinoderm* become sexually mature on the coast of Norway, to which its larvæ are transported by the gulf stream. The two sexually mature forms are apparently very distinct species, but to anyone who knows the young of the Mexican form, the Norwegian species is clearly only an immature condition of it, with fully developed sexual organs.*

Second. I have cited the rare appearance of wings in certain *Hemiptera*, in support of my views. The whole subject, however, of the correlations of the development of the sexual and cutaneous organs in insects is remarkably complex, but I will endeavour to put before you some of the more important facts bearing upon it.

It must be admitted, that the development of the female generative organs, and ova, has a very decided influence in arresting the development of cutaneous organs, in comparison with the development of the corresponding structures in the male.

It is not a little remarkable that, whilst in Vertebrates the male seems to require a higher elaboration (if I may use the term with a kind of indefinite meaning), for its development, so in insects, the female requires a larger supply of nourishment, and more favourable conditions.

* See Mr. Darwin's 'Descent of Man,' vol. ii. p. 215, for numerous other instances of this nature. Also Mr. Cope, 'On the origin of genera,' in Proc. Acad. Nat. Sc. Philadelphia, Oct. 1868; who I find has already arrived at similar conclusions on the effect of retardation and acceleration of sexual development, though I cannot follow his deductions.

In support of these statements, I will briefly bring one or two facts before you. Certain monstrous conditions in Vertebrates, in which almost all the parts of the body are doubled, are nearly, if not always, female; whilst in insects the male is sometimes developed agamically, as in the bee; and the males are usually smaller than the females.

Dr. H. Landois* published some very remarkable facts, which appear to me to have received considerably less attention than they deserve, owing to the flood of controversy, which originated in certain mistakes made by the author, and which led him to disbelieve in Parthogenesis.

Dr. Landois stated, that whole broods of some insects are often either entirely composed of males or females only. He affirmed that ill-fed larvæ always produced males, whilst well-fed ones usually produced females. In this there was clearly some error of observation, as it is a well-known fact, that the sex may be determined from an examination of the embryo long before it leaves the egg.

On the other hand, I am not inclined to look upon Dr. Landois' statement as altogether incorrect. The only insect I have ever bred in large numbers is the blow-fly, and I found that nearly all the insects bred from the large well-fed larvæ bought at the fishing-tackle shops were female, whilst ill-fed small larvæ have usually produced males. There may be an error in this observation, and it has occurred to me that it is possible the breeders of the maggots may pick out the largest larvæ, which are the females, for their best customers, the large shops: selling the smaller male larvæ to the smaller tradesmen. Still I cannot find that this is actually the case. From the large number of pupæ that always died, usually more than half, I am rather inclined to believe that a large supply of highly nutritive food may act injuriously on the male larvæ, especially if they are stimulated to feed by a higher temperature than the normal one, by causing an abnormal development, of the fat bodies for instance, at the expense of the structures destined to form the pupa. It is easy to understand why too little food would produce males only, as the females would perish before arriving at maturity.

* 'Zeitschrift für wissensch. Zool.,' Band 17, s. 375.

Dr. Landois, who has never, so far as I know, stated any clear and obvious facts incorrectly, although he has, unfortunately, drawn some very erroneous inferences, states very clearly that, when he half-starved his larvæ, males only were produced, but that when well-fed, there were many more females than males. Whatever the explanation may be, I am strongly inclined to give credit to the fact.

I mention these facts, because I believe that certain cutaneous appendages, as the gigantic mandibles and thoracic horns of many males, are complimentary to the sexual organs. That, in point of fact, they are produced by the excess of nutriment in the male, which, in the female, would go to form the generative organs and ova. It may be urged that this is an improbable explanation, but it does not appear so to my mind, when we remember the large amount of the generative product in the female, compared with that produced by the male.

I think it may be noticed, that all those insects which exhibit the cutaneous horns and great mandibles in the male, feed on wood and other vegetable substances, or decaying animal matters that afford a very limited amount of nutriment, which necessitates the laying by of great stores of nutriment by the female for the after-nourishment of her ova.* The males usually exhibit two tolerably distinct forms, one with very large mandibles or horns, and another with these organs scarcely larger than those of the female in the case of the mandibles, and very small in the case of thoracic horns, or other structures absent in the other sex.

It has occurred to me, that the males with the large cutaneous appendages may be those which are bred and nourished with the females, whilst those with the smaller horns may have been nourished by food not sufficiently nutritive to produce females. Hence the small horned males would have fewer offspring than the long-horned males; and the horns would tend continually to increase in size, although under bad or poor feeding in the larval condition, they may frequently be considerably reduced. I very much doubt if the theory of ornament and sexual selection can be applied to beetles, owing to the very

* These are chiefly developed from the great fat bodies of the female.

low development of their nervous system, although I should unhesitatingly apply it to the higher *Hymenoptera* and *Diptera*. I see, however, that Mr. Darwin has in his last work* applied the principle to account for the production of these horns.†

This long digression leads me to the wings of insects, which are really quite analogous to the cutaneous knobs and horns, so far as their relation to the nourishment of the body is concerned. The absence of wings in the female is well known to be excessively frequent, and there is no more remarkable instance, showing their relation to the female sexual organs, than the phenomena observed in *Aphis*.

The agamic *Aphides*, which have excessively imperfect female sexual organs, without either sperm sacs or collateral ‡ (shell-secreting?) glands, frequently have wings, whilst these never occur in those sexually perfect.

From all the above facts, I think it probable, that the apterous condition of female insects is an acquired one, dependent on the amount of nourishment received by the larva. I also think it highly improbable that the wings could have been developed by natural selection in one sex alone, without having been inherited by the other sex, in some few insects. And I think it more probable, that altered conditions of larval life, have gradually led to suppression of the wings in one sex, and that the winged forms are reversions to an anterior type.

Third. The early appearance of the sexual organs, their peculiar mode of development, and their occasional premature development, may now be considered.

* 'Descent of Man.'

† Closely related to this question, is the wider one of coloration in insects, and, as Mr. Darwin has suggested to me, the greater variability of the males than of the females. I have already noticed elsewhere, that the oxidization of the fat bodies of the larva of the blow-fly, produces the pigment with which the integument is coloured. The fat bodies also produce the material from which the sexual elements, as well as most of the tissues are nourished, hence the male element being much less than the female, more material remains for the development of colour and of the other organs. As the best fed forms are usually more variable, and as the amount of pigment is closely correlated with the conditions of the fat bodies of the larva, I think it probable that both coloration and variability may be directly influenced by sex, in the manner above indicated.

‡ I believe these glands in the fly, secrete the very hard, opaque egg-shell which surrounds the eggs when they are laid.

The facts I related at the commencement of this paper, referred exclusively to the *Ametabola*. I have not observed that the larvæ of the *Metabola* ever become truly sexually mature, but I think I shall be able to show that it is highly probable the phenomenon of viviparous generation in the gall-gnats, arises from the early maturation of the ovaries.

It has been already noticed that the sex of the *Metabola* may be discovered by an examination of the sexual organs of the embryo some time before birth. I have only observed the development of these organs in the blow-fly, and in this insect they are the only larval organs that are continuously developed, and which persist in the adult fly.

There are only three structures in the larva, which do not undergo disintegration during the development of the pupa. These are the imaginal discs, the nervous system, and the sexual organs. The imaginal discs do not persist in the perfect fly; they unite and form a pupa-skin, entirely homologous to the pupa-skin of a moth or butterfly; the dried larval skin becoming converted into a kind of cocoon. The nervous system undergoes rapid redevelopment, new structures being formed to subserve new functions; the sexual organs, alone, undergo ordinary development.*

I think we see the effect of the accelerated development of ovaries, in the viviparous agamic generation of Cecidomyian larvæ. Dr. Leuckart's† observations leave no doubt, in my mind, that the germ stocks of the Cecidomyian larva are actually modified ovaries, and that the development of the new larva, within the body of the mother, is the result of the non-development of the accessory sexual organs, the oviduct, vagina, &c. The agamic nature of the process is no objection to this theory, as we know that parthogenesis is by no means uncommon amongst perfect insects, even when they are ready to produce young in the ordinary way.

I cannot refrain from quoting Leuckart's own expression on this subject:—"The asexual propagation of the

* For further details, see my work on the 'Anatomy of the Fly.'

† Ann. Nat. History, 1866.

Cecidomyiidae unmistakeably approaches the phenomenon in *Aphides*; the only difference is, that the germ chamber of the Cecidomyian larva becomes detached, and moves about in the cavity of the mother; whilst in *Aphides*, the germ chambers remain permanently attached by an apparatus, which in form and arrangement, reproduces the conditions of the ordinary female organs."

In the agamic form of *Aphides*, we observe the same tendency to the non-development of the accessory sexual organs, in the absence of the spermathecae and collateral glands.

Lastly. With regard to the objection that the winged forms of insects are probably derived from the apterous or larval forms, I am far from being sure that such is really the case.

With respect to the *Metabola*, I think Gerstäcker, and others, have clearly shown that the larva is an acquired and not an original form.

If further evidence be needed on this point, I think it is afforded by the relation borne by the larva of the *Diptera* to the embryo and perfect insect. As this relation is highly remarkable, and as it is directly concerned in the conclusions I have arrived at on the relation of the larva of the *Metabola* and *Ametabola*, I will say a few words on the subject.

The embryo of the blow-fly, twelve hours after impregnation, bears a closer resemblance to the pupa, than it does at any subsequent period of larval life. During the remaining twelve hours of embryonic life, a very remarkable change takes place; all those parts of the embryo which correspond with the head of the perfect fly, become converted into the imaginal discs of Weismann; and do not again make their appearance externally until the pupa-state is assumed. This is quite analogous to the so-called hyper-metamorphosis of some *Coleoptera*: and especially reminds one of the manner of development in some *Crustacea*, where the embryo is surrounded, during development, by a kind of larval skin.

The embryos of *Ligia* and other Isopods, with their larva-like skin, afford, to my mind, a clue to the origin of the metamorphosis of the Insecta. Suppose the embryos

of these Crustacea to be born invested in their maggot-like integument, and to pass the first half of their existence in this condition, and we should have a condition very like that observed in the metamorphosis of the *Metabola*.

With regard to the primitive ancestral forms of the Insecta we know nothing; but I think there can be little doubt that they were nearly allied to the existing *Orthoptera*. Nevertheless, I think it quite probable, that the larva may have undergone even greater modifications than the imaginal forms, owing to the greater variability of the conditions to which larvæ are subjected.

I believe the great modification of the Insecta from their original type may, probably, have originated from modifications of the larva and imago re-acting on each other. The larva of one Ametabol form, *Aphis*, is known to reproduce agamically; a condition which I am not aware has ever been observed in a direct larva, but which occurs in acquired larval forms.

I have drawn up a table, which gives the views I have arrived at, concerning the relation of the various larval forms in the *Annulosa* and *Annuloida*. (*Vide* p. 202.)

The five spaces, one under the other, are intended to represent consecutive conditions. The forms in the lower lines in each column are supposed to have been produced by successive modifications from those above them in the same column. Thus the original larval and perfect forms of insects and trematoids are supposed to be unknown, and the pupa form is supposed to have been acquired before the present larval form.

In conclusion, I may say that I only look upon the hypothesis which has made the frame-work of my present paper, as highly probable. When it first occurred to me, I mentioned my ideas to Mr. Darwin; his kind encouragement, and the wish he expressed that I should publish my views were the main causes of my elaborating it to a greater extent. I then found it led me deeply into a most difficult labyrinth, which I have done my best to trace. I do not even think, myself, that I have established my main hypothesis, but I trust I have brought together the seed which may, ultimately, produce good fruit.

NOTE.—I would suggest, that some of the ideas I have thrown out concerning the horns of many *Lamellicorns*, might be easily worked out by some Entomologist living in the country, by rearing the insects, and watching the results with different kinds of food. In London, with much other work, I could not possibly undertake the care of large numbers of living insects.

CRUSTACEA.	INSECTA.		SCOLECIDA.	
	AMETABOLA	METABOLA	TREMATOIDA	
Inherited, or direct larva.	Unknown ancestral forms, perhaps represented by embryonic states, and hyper-metamorphosis.			Never producing young larvæ like <i>Cecidomyidæ</i> & <i>Cercaria</i> . Originally sexually mature like <i>Nauplius</i> , <i>Zoea</i> , &c.
Perfect form. }				Sexually mature.
	Imago.*	Imago.*	Adult form* (<i>Fluke</i>).	Sexually mature, sometimes reproducing agamically, like <i>Aphis</i> , and many other insects.
	Acquired larval form.	Acquired pupal form.	Acquired pupal form (<i>Cercaria pupa</i>).	Exhibiting a tendency to sexual maturity. The wingless condition of some moths may be looked upon as an acquired form approximating the pupa state.
		Acquired larval form.	Acquired larval form (<i>Cercaria</i>).	Sometimes reproducing larvæ, which ultimately produce the adult form, passing through the pupa state, like <i>Cercaria</i> , <i>Cecidomyidæ</i> .

* Highly modified from forms parallel with the adult Crustacea.